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# TAXONOMY OF THE WEST INDIAN CYCADS

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TEN GENERA of Cycadales exist in world floras. Four genera, all members of the Zamiaceae, are natives of the Western Hemisphere, and two of these are found in the West Indian region. The monotypic *Microcycas* (Miq.) A. DC. is endemic to Cuba, while *Zamia* L. is found from Mexico south to Bolivia and Brazil, as well as in the West Indias (Schuster, 1932). Within the West Indian region, cycads are indigenous to all of the Greater Antilles, the Bahamas, Florida, and the southeastern coast of Georgia but are absent from the Lesser Antilles and the Virgin Islands. Because of its restricted distribution and seeming morphological isolation, *Microcycas* has heretofore caused little dispute, but the taxonomic history of West Indian zamias, like that of many other West Indian plant groups (Howard, 1977), has comprised a confusing array of divergent circumscriptions and delimitations, resulting in widely different species tallies (from one (present study) to 14 or more (de Candolle, 1868)) for the region. Altogether, some 35 entities have been described, accounting for about 40 percent of the names proposed in the genus.

Diverse taxonomic treatments can be ascribed to complex variation patterns and political fractionation of the region, as well as to differences in philosophy among taxonomists. Most previous workers have had a very narrow species concept and have acknowledged neither extensive variation within populations nor continuity between populations. Often species were described on the basis of single specimens sometimes cultivated plants for which the original sources were unknown. Other than Schuster's (1932) synonymics, which are tortuous and partly invalid under the present *International Code of Botanical Nomenclature*, there has been little effort to consolidate nomenclature in different subregions, and nomenclatural and taxonomic chaos persist. This paper proposes a new taxonomy of West Indian cycads, based on field, herbarium, and garden studies: explains the contrast between this classification and those of previous workers; and accounts for most published names in the complex.

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#### TAXONOMIC AND NOMENCLATURAL HISTORY

West Indian cycads were described by pre-Linnaean authors, usually as species of "Palma," and Linnaeus (1763, 1764) founded his genus Zamia, with its sole species, Z. pumila L., on their descriptions and illustrations. Smith (1961) raised an important question concerning the typification of Z. pumila. He correctly contended that the Linnaean protologue contained references to two currently recognized species of Zamia, and that correct application of the name depended upon lectotypification by subsequent authors. Most authors have either rejected Z. pumila because of this mixture (e.g., Schuster, 1932) or have used it for the West Indian cycad described and illustrated by Commeliin (de Candolle, 1868; Carabia, 1941). Smith, in contrast, argued that Miller (1768) had first lectotypified the name using the other references. Thus, he contended that Z. punila L. should be applied to the Mexican species currently known as Z. furfuracea Aiton, and that the West Indian species that had almost universally borne the Linnaean epithet should be known as Z. debilis Aiton. This argument, which has largely been ignored, can be set safely aside within the framework of the ICBN. Miller's account need not be taken as a lectotypification of Z. pumila L. because it describes Palma pumila Miller and contains no reference to Linnacus's combination. Nomenclaturally, it can be considered an independent publication of the epithet. The first post-Linnacan use of Z. punila may be by Aiton (1789), who applied it (as a synonym) to a West Indian cycad. Zamia pumila L. may thus be retained for the common West Indian cycad that has traditionally been known (in part) by that name, and Z. furfuracea Aiton remains the correct name for a Mexican species.

Soon after the original description of Zamia, new West Indian species were added to the genus. Aiton (1789) contributed Z. debilis Aiton and Z. integrifolia Aiton, the latter a renaming of Z. punila L. With Z. media Jacq. and Z. angustifolia Jacq., Jacquin (1791, 1798) created the narrow species concept, based on leaflet widths, in West Indian Zamia. Aiton and Jacquin set trends followed by many later authors dealing with the taxonomy of Zamia in the West Indies-purposeful or inadvertent renaming of previously described entities, and proliferation of described taxa based on slight differences in leaflet width. As an example of the former trend, cycads with narrow leaflets from the south coast of the former Oriente Province of Cuba have successively been named Z. stricta Miq., Z. vatesii Miq., Z. angustissima Miq., Z. multifoliolata A. DC., and Z. guggenheimiana Carabia. Many plants attributable to these taxa are virtually indistinguishable from cycads from Eleuthera in the Bahamas named Z. angustifolia Jacq., and from others from Mayagüez Province, Puerto Rico, named Z. portoricensis Urban. The second trend is reflected in such epithets as Z. angustissima Miq., Z. angustifolia Jacq., Z. media Jacq., and Z. latifoliolata Prenl. The tendency toward a narrow species concept defined on leaflet width is even reflected in treatments of fossils of Zamia from the West Indies (Hollick, 1932). Additional names proposed in the last 200 years are included later in the synonymy of Z. pumila subsp. pumila.

Dwarf cycads from western Cuba were first distinguished as Zamia pygmaea Sims (1815). Since these diminutive cycads also display variations in leaflet size comparable to those of the more widespread larger plants, they too have engendered numerous specific epithets based on local variants. These names are included in the

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synonymy of Z. pumila subsp. pygmaea (Sims) Eckenw. in the taxonomic treatment presented below. The other Cuban endemic, Microcycas calocoma (Miq.) A. DC., was first described as a species of Zamia in 1851. Dc Candolle (1868) transferred it to a new monotypic genus because of its striking differences from the other species of Zamia then known. Its rarity and distinctiveness have inhibited recognition of segregates, and little controversy has attended taxonomic accounts of this species since its identity was firmly established (Caldwell & Baker, 1907).

Modern treatments of West Indian cycads adopt one of four differing points of view on the taxonomy of the Zamia pumila complex. 1) Each subregion has several species, which may or may not be shared between subregions (Schuster, 1932; Chamberlain, n. d.). This viewpoint is particularly attractive to botanists working within a single subregion and has characterized most treatments to date of West Indian cycads, including accounts for Florida (Small, 1933), the Bahamas (Britton & Millspaugh, 1920), Puerto Rico (Britton & Wilson, 1926), and Cuba (León, 1946; Liogier, 1969). It is less attractive when viewed against overall variation in the West Indian region. 2) Each subregion has a single endemic species (Read, 1967). This view ignores parallel variation in cycads of different subregions, particularly in Cuba, Puerto Rico, and the Bahamas. 3) The West Indian region has a single endemic species of Zamia. This is the viewpoint adopted here and rests on evidence presented below. It is more conservative than treatments such as that of Carabia (1941), which accept two or three species and are intermediate between viewpoints 1 and 2. 4) West Indian cycads are conspecific with those of the Central and South American mainland, W. C. Steward (pers. comm.) contends that Zamia is monotypic. This concept of Z. pumila ignores apparent discontinuities in variation to include a wide array of diversity in morphology, ecology, and chromosome number under one specific epithet. Since Steward's arguments are not yet published, they can not be examined in detail here. Of the four taxonomic viewpoints enumerated above, numbers 2 and 4 do not seem to accord with the facts of variation in West Indian zamias, as seen here. Based on information presented below, a treatment reflecting viewpoint 1 must embody great arbitrariness in delimitation of taxa. I favor a conservative approach (number 3) as most workable and most in accordance with present variation in these plants.

#### MATERIALS AND METHODS

Approximately 1500 herbarium specimens (including 33 holotypes and isotypes) of *Microcycas* and *Zamia* from throughout the West Indian region were examined in the following herbaria: A. AMI, BM, DAO, DAV, DUKE, F. FAU, FLAS, FM, FTG, GA, GH, MCH, MO, SWL, XCU, NY, TEX, UC, UNC, US, USF, and the personal herbarium of Dr. J. de Js. Jiménez (Santiago, Dominican Republic). Over 500 living plants at Fairchild Tropical Garden, representing 34 accessions from known localities in all West Indian subregions and including a few interpopulational hybrids, were also studied. Field work in the Bahamas and throughout Florida complemented the herbarium and garden studies and provided information concerning the association of morphological variations with habitat differences. Occurrences were mapped, and leaflet length, width, and vein number (characteristics that dominated previous species delimitations) were JOURNAL OF THE ARNOLD ARBORETUM [vol. 61

recorded. Variation in these characters is analyzed below. Additional morphological features, both vegetative and reproductive, were recorded; they also influenced taxonomic decisions. They are not specifically analyzed below but are summarized in the taxonomic descriptions presented. The short lists of representative specimens come from the full range of each taxon and emphasize morphological variation within those subregions in which each occurs.

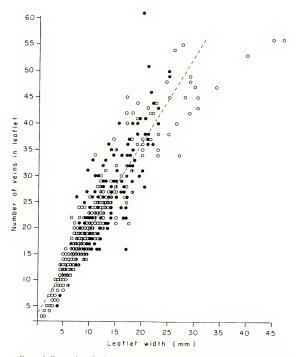


FIGURE 1. Regression of vein number on leaflet width of West Indian zamias: circles, Zamia punila subsp. punila; spots, subsp. pygmaca; mixed symbols, both subspecies: regression line dashed, y = 1.66x + 3.29,  $r^2 = 0.88$ , n = 1111.

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### RESULTS AND DISCUSSION

Previous workers, often lacking fertile material, emphasized leaflet characteristics in their specific delimitations of West Indian zamias. Because leaflet length, width, and vein number differ between populations, these (especially the latter two) are the features that were most often used to distinguish new species. Furthermore, since early workers had few specimens available to them, their descriptions included narrow ranges of variation in these characters, and later authors continued this tradition (Read, 1967). A scatter diagram of the two most frequently used distinguishing characters (leaflet width and vein number), based on a representative sample of 500 specimens, shows them to be closely associated (FRGME 1). The correlation coefficient for these characters for all 1043 specimens measured is 0.94, and similar high correlations characterize plants from each of the West Indian subregions (TABLE 1). Thus, 88 percent of the variation in vein number in these cycad leaflets is accounted for by corresponding differences in leaflet width. It is not surprising, therefore, that authors could always find differences in vein number to reinforce differences in leaflet width. In fact, the features are structurally related: no matter

 $T_{\text{ABLE}}$  1. Correlation coefficients of leaflet width with vein number and leaflet length for Zamia in the West Indian region.†

REGION	VEIN NUMBER	n	LEAFLET LENGTH	n
West Indies	0.94***	1043	0.07*	1083
Florida	0.93***	401	0.16**	345
Bahamas	0.97***	69	0.45***	106
Cuba	0.91***	364	0.10*	427
Jamaica	0.86***	11	0.24 n.s.	19
Dominican Republic	0.81***	31	0.31*	46
Puerto Rico	$0.94^{***}$	167	0.21*	130

\* Correlation coefficients significant at: \*p<.05, \*\*p<.01, \*\*\*p<.001.

how wide or narrow the leaflets are, there are always about two veins per mm. of width. These veins arise by numerous dichotomies of two original traces from the rachis within the first 4 mm. after they enter the petiolule. Rarely, dichotomies may occur before the traces enter the leaflet, so that three or four traces enter, but this is as frequent in narrow leaflets as in wide ones. Thus, two traces enter most leaflets, and these ramify to maintain a relatively constant relation of vascular tissue to other tissues of the blade. Cycad taxonomists were incorrect in using differences in these features as independent differences between West Indian Zania species, and leaflet width will be emphasized in subsequent analyses in this paper.

In contrast to leaflet width and vein number, a scatter diagram of leaflet width vs. leaflet length (FiGURE 2) shows no obvious association, and the low, but mostly significant, correlation coefficients (TABLE 1) argue for the independence of these features within each subregion, as well as within the entire West Indian area. Leaflet length seems, instead, to reflect the general robustness of the plant. For instance, the correlation coefficient of leaflet length with total leaf length is 0.70, and other features and also associated in a loose group of "size" characters that are indepen-

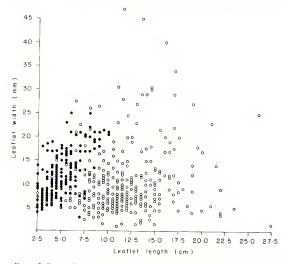


FIGURE 2. Scatter diagram of leaflet width vs. leaflet length of West Indian zamias: circles, Zamia pumila subsp. pumila; spots, subsp. pygmaea; mixed symbols, both subspecies; n = 500.

dent of a series of characters associated with leaflet width (Eckenwalder, in prep.), Therefore, leaflet length is used in addition to leaflet width to represent these two sets of vegetative characters in the analyses that follow:

When leaflet widths of individuals are plotted in frequency histograms for the West Indies and for each of its subregions (Ficure 3), it is apparent that these frequencies follow smooth distributions within areas and sum to a smooth, unimodal distribution for the entire region. These frequency distributions provide little support for recognition of many taxa in the region, a point emphasized by superimposing ranges of leaflet width of species accepted for the West Indies by the most recent comprehensive monographs (Schuster, 1932; Chamberlain, n. d.) onto the overall West Indian histogram (Ficure 4). Morphological boundaries between taxa accepted by these authors are clearly arbitrary, and the modal width for cycads of the region (6.5-7.5 mm.) is not even included in values for any of Chamberlain's species. If species boundaries are not recognizable in these data, Schuster's further segregation of these cycads among several subsections of the genus seems even less warranted.

Data on leaflet length show a similar trend of smooth distributions within subre-

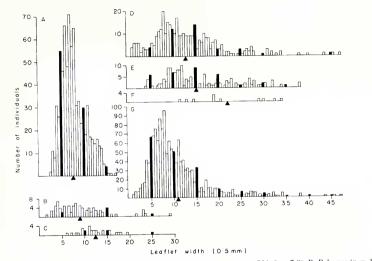


FIGURE 3. Histograms of leaflet widths of zamias of the West Indian region: A. Florida (n = 754,  $\tilde{x} = 7.8$ ); B. Bahamas (n = 100,  $\tilde{x} = 9.1$ ); C. Dominican Republic (n = 31,  $\tilde{x} = 12.7$ ); D. Cuba (n = 364,  $\tilde{x} = 13.1$ ); E. Puerto Rico (n = 167,  $\tilde{x} = 15.4$ ); F, Jamaica (n = 11,  $\tilde{x} = 22.4$ ); G, entire West Indian region (n = 1427,  $\tilde{x} = 10.5$ ); triangles mark locations of means.

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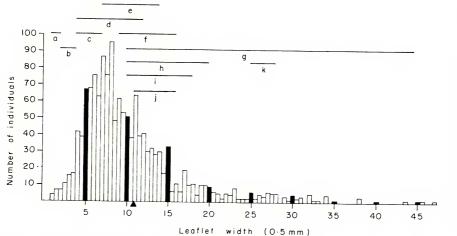


FIGURE 4. Ranges of leaflet width given by Chamberlain (n. d.) for West Indian species of Zamia superimposed on frequency histogram of leaflet widths for the entire West Indian region: a, Z, angustissima; b, Z, angustifolia; c, Z, floridana; d, Z, pygmaea; e, Z, silicea; f, Z, media; g, Z, Laitfoliolata; h, Z, portoricensis; i, Z, kickxii; j, Z, pumila; k, Z, ottonis (d, e, i, and k are synonyms of Z, pumila) subsp. pumila).

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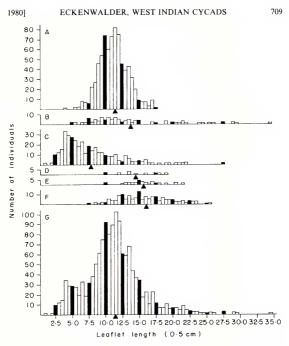


FIGURE 5. Histograms of leaflet lengths of zamias of the West Indian region: A, Florida (n = 754,  $\bar{x} = 11.3$ ); B, Bahamas (n = 100,  $\bar{x} = 13.5$ ); C, Cuba (n = 364,  $\bar{x} = 7.6$ ); D, Jamaica (n = 11,  $\bar{x} = 14.4$ ); E, Dominican Republic (n = 31,  $\bar{x} = 15.5$ ); F, Puerto Rico (n = 167,  $\bar{x} = 15.9$ ); G, entire West Indian region (n = 1427,  $\bar{x} = 11.1$ ); triangles mark locations of means.

gions and overall for the West Indies (FiGURE 5). In Cuba, however, cycads I have distinguished as Zamia pumilia subsp. pygmaea contribute to a bimodal distribution of leaflet length. In their extreme form in westernmost Cuba, these smaller plants appear strikingly different from individuals of subsp. pumila from eastern Cuba, but there is an uninterrupted cline of intergradation in robustness across the length of the island (FiGURE 6). This cline steepens at the border between the two subspecies in eastern Cuba (MAP 1), so that most individuals can be readily identified to subspecies. With this exception, leaflet length. like leaflet width, provides little evidence

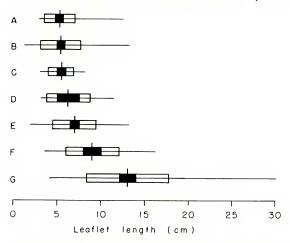
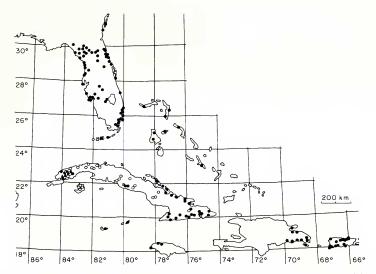


FIGURE 6. Dice-grams of leaflet lengths of Cuban zamias from west to east across island by old provinces: A, Isla de Pinos (n = 61,  $\tilde{x} = 5.2$ ); B, Pinar del Río (n = 127,  $\tilde{x} = 5.4$ ); C, Habana (n = 34,  $\tilde{x} = 5.4$ ); D, Matanzas (n = 16,  $\tilde{x} = 6.2$ ); E, Las Villas (n = 130,  $\tilde{x} = 7.0$ ); F, Camagúey (n = 37,  $\tilde{x} = 9.0$ ); G. Oriente (n = 112,  $\tilde{x} = 13.1$ ). Horizontal line = range; vertical line = mean; large rectangle = twice the standard deviation; small rectangle = four times the standard deviation of mean.

favoring segregation of taxonomic entities among West Indian zamias.

Other characters examined, both vegetative and reproductive, also show continuous variation patterns that discredit the traditional recognition of numerous taxonomic segregates, but I have concentrated on those emphasized by previous workers. Particular combinations of features characterize many distinctive local populations that have been described as species in previous taxonomic treatments. For example, individual islands of the Bahamas have populations of Zamia differing markedly in appearance (Fiotures 7, 8; Eckenwalder, in press), and these populations were divided among four species by Britton and Millspaugh (1920). Similarly, Small (1933) recognized four species of Zamia in Florida, where plants of coastal hammocks in the northeast (Z. unbraves Small) seem sharply distinct from those of the remainder of the peninsula (Z. floridana A. DC.). But distinctive local races that appear to maintain their integrity in particular subregions seem much less distinct in the context of total variation throughout the West Indies. Formal recognition of these variants would be difficult to achieve consistently without further multiplying de-



MAP 1. Distribution of native West Indian cycads: spots, Zamia pumila subsp. pumila; circles, subsp. pygmaea (Cuba only); mixed symbols, intermediates (Cuba only); triangles, Microcycas calocoma (Cuba only).



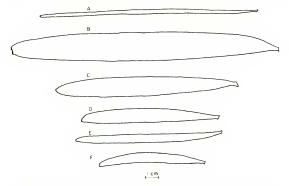


FIGURE 7. Outlines of representative leaflets of Bahamian zamias: A, Eleuthera (*Correll & Hill 45240, mi*); B, Long Island (*Britton & Millspaugh 6271, Git—isotype of Zamia lucayana*); C, Grand Bahama (*Britton & Millspaugh 2576, +*); D, Great Abaco (*Correll et al. 42713, FTG*); E, New Providence (*Britton & Brace 704, NY*); F, Andros (*Brace 6990, +*).

scribed entities and would not clarify the biological situation. The distribution of variants is complicated by effective dispersal by both birds and seawater (Eckenwalder, 1980), which has confused what may once have been a more straightforward situation. Now, however, the variation pattern within *Z. pumila* seems taxonomically irresolvable (making the species an ochlospecies, as described by White, 1962, and by Whitmore, 1975), and the course adopted here is to describe and accept variability without formalizing it in a necessarily arbitrary infraspecific hierarchy like that of Schuster (1932).

#### TAXONOMIC TREATMENT

#### KEY TO INDIGENOUS WEST INDIAN CYCADS

- Stems largely subterranean; leaves few, 3 to 12 per crown, 1–8(−15) dm. long, with petiole ca. ½ total length of leaf: leaflets horizontally spreading or ascending, linear, oblong, oblanceolate to obovate, rarely lanceolate, usually blint, usually with few to many callose tech apically, articulated to rachis by callose

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petiolule 2-5 mm. wide; male and female cones with purple or rusty pubescence, compact, 0.2-2.5 dm. long, peduncle at least 1/3 length of cone; scales of male and female cones with flat, truncate apex; fleshy layer of seed orange or red.

- 2. Plants robust, stems 2.5 cm. or more in diameter; leaves 4-8(-15) dm. long; leaflets 5-25(-35) cm, long, usually linear or oblong, usually revolute with thickened margin, thick and leathery; cones 0.5-2.5 dm. long. .....
- 2. Plants dwarfed, stems 2.0 cm. or less in diameter; leaves 0.3-6(-10) dm. long; leaflets 2.5-7(-10) cm. long, often obovate, margin thin, thin and fragile; cones 0.2-1.0 dm. long. ..... Z. pumila subsp. pygmaea.

#### Microcycas calocoma (Miq.) A. DC. Prodr. 16(2): 538. 1868.

Zamia calocoma Miq. in Van Houtte, Fl. Serres Jard. Eur. 7: 141. 1851. Type: Cuba, cult. Hort. Amstelod., Mignel s.n. (holotype, 1).

ILLUSTRATIONS: Caldwell, Bot. Gaz. (Crawfordsville) 44: figs. 10-14. 1907; Caldwell & Baker, Bot. Gaz. (Crawfordsville) 43: fig. 1. 1907; Schuster, Pflanzenr. 99: figs. 6P, 8K; pl. 5. 1932.

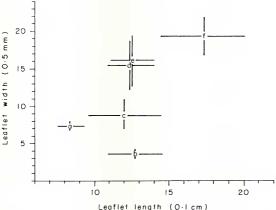


FIGURE 8. Plot of means of leaflet width ( $\bar{y}$ ) vs. leaflet length ( $\bar{x}$ ) for zamias from different Bahamian islands: a, Andros (n = 27,  $\bar{x} = 8.4$ ,  $\bar{y} = 7.3$ ); b, Eleuthera  $(n = 24, \bar{x} = 12.7, \bar{y} = 3.6); c$ , New Providence  $(n = 9, \bar{x} = 12.0, \bar{y} = 8.8);$ d, Great Abaco (n = 11,  $\bar{x} = 12.4$ ,  $\bar{y} = 15.4$ ); e, Grand Bahama (n = 18,  $\bar{x} = 12.5$ ,  $\bar{y} = 16.1$ ; f, Long Island (n = 17,  $\bar{x} = 17.3$ ,  $\bar{y} = 19.3$ ); horizontal and vertical lines represent twice the standard error on each side of mean.

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Arborescent, sparingly branched cycads up to 20 m, tall; crown formed by 10 to 50 pinnate leaves; leaves 1-2 m. long, emerging in annual flushes, covered by transient, mealy, tamy pubscence; leaflets 50 to 80 pairs, 8–20 cm, long, lanccolate, reflexed, caducous after 1–3 years from more persistent rachis, the rachis falling after 4 or 5 years, leaving an armor of persistent leaf bases that eventually abscise, the older portions of trank developing shallowly furrowed, thin bark; male and female cones annual, 1 or 2, emerging from among scale leaves of crown, massive, 4–7 dm, long, with 500 to 1500 peltate hexagonal scales in ca. 20 straight rows, the external face tawny-pubescent, with raised, rounded knob; outer fleshy layer of seed coat light pink, turning peach at maturity, seed 2.5–3 cm, long. n = 13 (Sax & Beal, 1934).

DISTRIBUTION Endemic to woodlands of canyons and foothills of the Sierra del Rosario in Pinar del Río Province, western Cuba (MAP 1), where it is apparently rare (Caldwell, 1926). Although the species is in little immediate danger of extinction because it is not commercially exploited and because the slopes on which it grows are unsuitable for cultivation, it is listed in Appendix 1 of the International Convention on Trade in Threatened and Endangered Species (Ayensu & DeFilipps, 1978).

REBRISISINATIVE SPECIARISS Cuba, PINAR DEL RIO Britton et al. 9637 (NY), Ekman 10845 (US), 18166 (NY), Shafer 13750 (NY, US), 13882 (NY, US), Van Hermann 3322 (NY, US).

*Microcycus* is scarcely differentiable from *Zamia*. When this Cuban endemic was first elevated to generic rank by de Candolle (1868), the majority of known species of Zamia were low, West Indian or Mexican plants that were superficially very different in stem, foliage, and cone from the massive Z. calocoma. Later, chromosome counts of n = 8 for species retained in Zamia seemed to confirm their isolation from the n = 13 Microcycas (Sax & Beal, 1934). Embryological features, as well as the greater number of both spermatozoids and archegonia, were unique to Microcycas among all cycads studied and also reinforced separation of the two genera (Chamberlain, 1935). The only character used to separate the two genera in generic keys to the cycads, however, has been the flattened knob of the male cone scales of Microcycas, compared to the truncate microsporophyll of Zamia (de Candolle, 1868; Schuster, 1932). In recent years, increasing access to arborescent species of Zamia from forests of Central and South America have eliminated many apparent differences between Zamia and Microcycas. Living plants of these formerly little-known species are becoming available for study at Fairchild Tropical Garden and other institutions. The taxonomy of these species is unresolved, but some of them have individual leaf and leaflet or cone characteristics of M. calocoma. None duplicates the combination of characters found in the Cuban cycad, but collectively they possess all of the gross morphological features formerly thought to distinguish Microcycas from Zamia. Zamia, formerly considered to be chromosomally uniform with n = 8, has been shown to have a diversity of chromosome numbers up to the u = 13 formerly thought to be confined among cycads to Microcycas (Norstog, 1974, and in press). Recent anatomical work has further shown that Zamia and Microcycas share an unusual branched hair type not found in other cycads, including the related genus Ceratozamia Brongn. (D. W. Stevenson, pers. comm.). The only features now

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remaining that distinguish the two genera are the extreme proliferation of both archegonia and spermatozoids in *Microcycas*. Embryology of the arborescent zamias of Tropical America is virtually unknown (Norstog, 1977), and a decision to return *M. calocoma* to the genus Zamia, although likely in the future, should await embryological investigation of *Z. chigua* Seem. and its allies. *Microcycas calocoma* was probably isolated in the West Indies by the same events that isolated *Z. pumila*. It has probably diverged from Central American arborescent zamias just as *Z. pumila* diverged from its closest relatives in the Central American *Z. furfuracea* complex.

#### Zamia pumila L. subsp. pumila

- Zamia pumila L. Sp. Pl. ed. 2. 2: 1659. 1763. LECTOTYPE Palma prunifera humilis non spinosa, insulae hispaniolae, fructui jujubino similis, ossiculo triangulo, J. Commelijn, Horti Med. Amstelod. 1: r. 58. 1697 (lectotype, AMS; imprints. Hunt Inst.], sv]. Palmifolium pimilium (L.) Kuntze, Rev. Gen. Pl. 2: 803. 1891. Zamia debilis Aiton, Hortus Kew. 3: 478. 1789, nomen illegii. Palmifolium debile (Aiton) Kuntze, Rev. Gen. Pl. 2: 803. 1891. Zamia humilis Salisb. Prodr. 400. 1796, sphalm. Zamia media var. commeliniana Schuster, Pflanzent. 99: 155–157. 1932.
- Zamia integrifolia Aiton, Hortus Kew. 3: 478. 1789. TYPE Florida, cult. Kew, Aiton s.n. (holotype, nst: tracing, sv!). Palmifolium integrifolium (Aiton) Kuntze, Rev. Gen. Pl. 2: 803. 1891. Zamia floridana var. purshiana Schuster, Pflanzenr. 99: 151. 1932.
- Zamia angustifolia Jacq. Ic. Pl. Rar. 3: t. 636. 1791. Type: Bahamas, cult. Hort. Vindob. (lectotype, pl. 636). Pahnifolium angustifolium (Jacq.) Kuntze, Rev. Gen. Pl. 2: 803. 1891.
- Zamia media Jacq. Pl. Rar. Horti Caes. Schoenbr. 3: 77, 78. tt. 397, 398. 1798.
   Typi: West Indies, cult. Hort. Schoenbr. (lectotype, pl. 398). Palmifolium medium (Jacq.) Kuntze, Rev. Gen. Pl. 2: 803. 1891. Zamia media var. jac-quiniana Schuster, Pflanzenr. 99: 157. 158. 1932. nomen illegit.
- Zamia tenuis Willd, Sp. Pl. ed. 5, 4: 846. 1806. Type Bahamas, cult. Hort. Berol., Willdenow s.n. (holotype, n. isotype (frag.), syl). Palmifolium tenue (Willd.) Kuntze, Rev. Gen. Pl. 2: 803. 1891. Zamia media var. tenuis (Willd.) Schuster, Pflanzen: 99: 158. 1932.
- Zamia dentata Voigt, Syll, Pl. Nov. 2: 53, 1828.
- Zamia angustissima Miq. Nieuwe Verh. Eerste KI. Kon. Ned. Inst. Wetensch. Amsterdam, ser. 3. 4: 184. 1851. Type trop. Amer. [Cuba], cult. Hort. Amstelod., Miquel s.n. (holotype, t.). Zamia angustifolia var. angustissima (Miq.) Regel, Gartenflora 27: 13. 1878. Palmifolium angustissimum (Miq.) Kuntze, Rev. Gen. Pl. 2: 803. 1891.
- Zamia stricta Miq. Nieuwe Verh. Eerste Kl. Kon. Ned. Inst. Wetensch. Amsterdam, ser. 3. 4: 183. 1851. TYPE trop. Amer. [Cuba], cult. Hort. Amstelod., Miquel s.n. (holotype, 1.). Zamia angustifolia var. stricta (Miq.) Regel, Gartenflora 27: 13. 1878. Palmifolium strictum (Miq.) Kuntze, Rev. Gen. Pl. 2: 803. 1891.
- Zamia yatesii Miq. Nicuwe Verh. Ecrste KI. Kon. Ned. Inst. Wetensch. Amsterdam, ser. 3. 4: 182. 1851. Type trop. Amer. [Cuba], cult. Hort. Amstelod., Miquel s.n. (holotype, L). Zamia angustifolia var. yatesii (Miq.) Regel, Garten-

flora 27: 13. 1878. Palmifolium yatesii (Miq.) Kuntze, Rev. Gen. Pl. 2: 803. 1891.

- Zamia floridana A. DC. Prodr. 16(2): 544. 1868. LECTOTYPE E. Florida, Fort Brooke, Hulse s.n. (holotype, GDC; isotype, sv!). Zamia angustifolia var. floridana (A. DC.) Regel, Gartenflora 27: 13. 1878. Palmifolium floridanum (A. DC.) Kuntze, Rev. Gen. Pl. 2: 803. 1891.
- Zamia multifoliolata A. DC. Prodr. 16(2): 545. 1868. Type Cuba [Oriente], San Juan de Buenavista, Wright 597 (holotype, GDC isotypes, GU, MO, NY, US). Palmifolium multifoliolatum (A. DC.) Kuntze, Rev. Gen. Pl. 2: 803. 1891.
- Zamia latifoliolata Prenl. Bull. Soc. Vaud. Sci. Nat. 11: 278. 1872. Type: Republica Dominicana, road to Punto de la Torreeilla, *Prenleloup s.u.* (holotype, LAU).
- Zamia concinna Hort. Booth ex Regel, Gartenflora 27: 9. 1878, nomen inval. (pro syn. Z. pumila L.).
- Zamia cylindrica Hort. Booth ex Regel, Gartenflora 27: 9. 1878, nomen inval. (pro syn. Z. punila L.).
- Zamia linifolia Hort. Pawl. ex Regel, Gartenflora 27: 13. 1878, nomen inval. (pro syn. Z. angustifolia Jacq.).
- Zamia linearifolia Linden, III. Hort. 28: 32. 1881, nomen nudum.
- Zamia portoricensis Urban, Symb. Antill. 1: 291. 1899. Type Puerto Rico, Mayagüez, prope Guanica in sylva ad Ensenada. Sintenis 3782 (holotype, n. isotype (frag.), syl). Zamia media var. portoricensis (Urban) Schuster, Pflanzenr. 99: 158. 1932.
- Zamia allison-armourii Millsp. Publ. Field Columbian Mus., Bot. Ser. 2: 23, 1900. Type Republica Dominicana, Distrito Nacional, near river flowing into Santo Domingo, *Millspaugh 817* (holotype, F!; isotype, sy!).
- Zamia erosa Cook & Collins, Contr. U. S. Natl. Herb. 8: 267. 1903. LECTOTYPE (here designated): Puerto Rico, Ponce, Coamo Springs, *Cook s.n.* (lectotype, sv!: isolectotype, sv!).
- Zamia lucayana Britton, Bull. New York Bot. Gard. 5: 311. 1907. Type. Bahamas, Long Island, Clarence Town and vicinity, *Britton & Millspaugh* 6271 (holotype, svl; isotypes, rl, GB!, svl).
- Zania umbrosa Small, J. New York Bot. Gard. 22: 136, 1921. LECTOTYPE (here designated): Florida, Volusia, Daytona Beach, Small 8679 (lectotype, sv1; isolectotype, NUK!, FLAS!, oil).
- Zamia silvicola Small, J. New York Bot. Gard. 27: 128. figs. 1, 2, 1926. Type Florida, Citrus, "Spanish Mound" near Crystal River, Small, Small, & DeWinkeler 10060 (holotype, sy!). Zamia floridana var. purshiana f. silvicola (Small) Schuster, Planzenr, 99: 152, 1932.
- Zania brachyphylla Hort, ex Schuster, Pflanzenr. 99: 159, 1932, nomen inval. (pro syn. Z. angustifolia Jacq.),
- Zannia linearis Miq. ex Schuster, Pflanzenr. 99: 159. 1932, nomen inval. (pro syn. Z. angustifolia var. yatesii (Miq.) Regel).
- Zamia media var. gutierrezii f. calcicola Schuster. Pflanzenr. 99: 155, 1932. Type Cuba, Pinar del Río, Baños de San Vicente, Britton, Britton, & Gager 7392 (holotype, B. isotypes, Gil, sv!). Zamia calcicola Britton ex Schuster, Pflanzenr.

- 99: 155. 1932, nomen inval. (pro syn. Z. media var. gutierrezii f. calcicola Schuster).
- Zamia media var. jacquiniana f. brevipinnata Schuster, Pflanzenr. 99: 158. 1932. LECTOTYPE (here designated): Cuba, Oriente, Holguín to Myabe, Shafer 1406 (lectotype, B: isolectotypes, F!, NY!).
- Zamia subcoriacea Wendl. ex Schuster, Pflanzenr. 99: 155. 1932, nomen inval. (pro syn. Z. media var. commeliniana Schuster).
- Zamia verbruggiana Hort. ex Schuster, Pflanzenr. 99: 159. 1932, nomen inval. (pro syn. Z. angustifolia var. yatesii (Miq.) Regel).
- Zamia guggenheimiana Carabia, Caribbean Forest. **2:** 89. 1941. Type: Cuba, Oriente, Pilón, Ensenada de Mora, Manzanillo, *Carabia 1403a* (holotype, sy!; isotype, F!).

LLUSTRATIONS: Small, J. New York Bot. Gard. 27: figs. 1, 2, 1926; Victorin & León, Itin. Bot. Cuba, figs. 33-37, 283, 284, 1942.

Cycads with short, preponderantly underground stems, 2.5–6 cm. in diameter, these often highly branched in apparent dichotomics; crown formed by (1 to) 4 to 8 (to 12) pinnate leaves; leaves (1–)3–7(–16) dm. long, emerging in annual or irregular flushes, covered by transient, rusty, filamentous pubescence; the leaflets (2 to) 10 to 30 (to 45) pairs, (4–)8–20(–35) cm. long, linear, lanceolate, oblong, or oblanceolate, horizontally spreading to secund, caduceous after 1 or 2 years, only shortly before rachis, rachis abscissing with leaf bases to leave smooth stem; male and female cones annual, long peduncled, with peltate, hexagonal scales in vertical files, the external face of scales rusty or dark purple pubescent, faceted, with flat center, the male cones 1 to 8 (to 63), emerging from among inner leaves of rows, 4–6.5(–13) cm. long, with 9 to 15 scales in each of 6 to 11 rows, the female cones solitary, terminal, more massive than males, 6-10(-20) cm. long, with 3 to 5 scales in each of 5 or 6 rows; outer fleshy layer of ovular seed coat pink, turning bright orange or red at maturity, seed |-2.5 cm. long, n = 8 (Sax & Beal, 1934).

DISTRIBUTION. Found sporadically throughout the native range of cycads in the West Indian region, but absent from Haiti and many of the Bahamas and rare in western Cuba, where it is replaced by subsp. *pygmaca* (see MAP 1). It occurs in a variety of habitats ranging from open sea bluffs and sand dunes. through pine and oak savannas, to closed-canopy oak hammocks and tropical forests. It is most common near sea level on limestone and sand but also occurs on other substrates. Morphological features of leaflet width, attitude, and thickness are associated with habitat differences, apparently affected by both genetic and environmental components (Eckenwalder, unpubl. data). The plants are frequently cultivated for ornament in their native regions and were formerly the basis of a starch-extraction industry (Small, 1921). Habitat destruction is the major current threat to them, especially in Florida, where residential development is leading to a drastic decline in number. The subspecies is listed as threatened in Florida (Ward & Pritchard, 1979).

REPRESENTATIVE SPECIMENS Florida. ALACHUA Small 8450 (MO. NCU. NY), D. & S. Ward 1838 (FLAS. FSU. NCU. US. USF), Weber S.N. (F. NY. US). BROWARD Moldenke 504

(DUKE, MO, NY), Sandler s.n. (FAU), Seibert 1168 (A, MO), CETRUS Baltzell 4724 (FLAS), Lakela 26820 (USF), Small 10387 (NY). DADE Beckner 1775 (FLAS, FSU, USF), Curtiss 2676 (A. GA. GH. MO. NY. US. USF), Demarce 10237 (MO. UC. US), Tracy 9265 (F. GH. MO. NY. TEX. US). DIXIE: Harbison 57 (A, NCU, US). GILCURIST Ward & Ford 3588 (FLAS, NCU, USF). GLADES Ward et al. 2423 (FLAS, GILUSE). HERNANDO Small et al. 10067 (DUKE, MO. NCU, NY). HILLSBOROUGH. Blanton 6921 (F. MO, US). LEVY EVERS S.N. (FLAS), Godfrey & Redfearn 52834 (DUKE, FSU, GH, NY, USF), Miller 339 (US), Murrill s.n. (MO). MARION Mather M-172 (FLAS. GA), Norstog s.n. (NY. USF), Schuster A-258-a (DUKE, FSU), ST. JOHN'S Smith 522 (F. GH. US), Ward & Moore 2362 (FLAS, FSU, NCU, USF), SARASOTA, Simpson 394 (F. GH. NY. US). SEMINOLE Beckner 884 (FLAS. FSU. GA). TAYLOR. Godfrev & Redfearn 52817 (DUKE, FSU, GH, NCU, NY, UC, USF). VOLUSIA. Brown s.n. (NCSC), Curtiss 2676b (F. GA. MO. NY. US. USF), Read 1046 (A. FTG), Small 8679 (DUKE, FLAS, GH. NY), Georgia. CAMDEN Proctor s.n. (GA). GLYN. Duncan 23659 (GA). Bahamas. GREAT ABACO Brace 1746 (F. NY), Correll et al. 42577 (FTG). ANDROS Brace 6990 (F. NY), Hill 3183 (F. FTG. NY). ELEUTHERA Britton & Millspaugh 5418 (F. NY. UC. US), Correll & Hill 45240 (F. FTG. LL. MO. NY). GRAND BAHAMA Brace 3693 (F. GH. MO. NY, US), Britton & Millspaugh 2576 (F. NY. US). LONG ISLAND Hill 828 (F. GH. MO. NY. US), 2334 (FTG. NY). New Providence: Britton & Brace 704 (F. NY). Cuba. CAMAGUEY, Shafer 679 (F. NY. US), 793 (F. NY. US), 2659 (F. NY. US). ISLA DE PINOS Carabia 1190 (F). LAS VILLAS Britton & Wilson 5443 (F. NY), Gonzales 381 (A), León & Carabia 19074 (F), Shafer 12198 (NY, US). MATANZAS Carabia 1992 (1). ORIENTE Britton & Cowell 12742 (MO, NY. US), Carabia 3523 (F), Hioram 4924 (F. GII. NY), León & Alain 18934 (F. GII), Pollard & Palmer 141 (F. GH. MO. NY. US), 382 (F. GH. MO. NY. US), Shafer 1406 (F. NY. US), Victorin 60037 (GH. MO, NY, US), Wright 1463 (F. GH. MO), PINAR DEL RIO: Baker 28944 (NY), Carabia 3189 (F), Van Hermann 7153 (F. GR), Jamaica, St. ANN Clift s.n. (FTG), Howard & Proctor 15114 (A), TRELAWNY Proctor 31556 (F. GH. LL), WESTMORELAND: Britton & Hollick 2070 (NY), Clift s.n. (FTG), Harris 10229 (NY, US), Cayman Islands. GRAND CAYMAN Kimbe s.u. (FTG), Osment s.n. (FTG). Dominican Republic. Altagracia R. & E. Howard 9774 (GILNY, US), Liogier 12341 (GILNY, US). DISTRITO NACIONALI Allard 13572 (US), Ekman 5800 (GILUS), Rose et al. 3783 (NY.US). ROMANA: Crafts 115 (DAV), Miller 1001 (US), Taylor 352 (F.NY), SAMANA: Abbott 1158 (US), Liogier 14383 (NY. US). SAN PEDRO DE MACORIS Augusto 691 (NY), R. & E. Howard 9494 (GR), Rose et al. 3707 (F. NY. US). SEIBO Jiménez 5052 (NY), Miller 1014 (US), Taylor 112 (NY). Puerto Rico, AGUADELA N. & E. Britton 9282 (NY), ARECIBO Blomquist 11984 (DAV. DUKE, MO, TEX), Stimson 3816 (DUKE, MICH, MO, NY), Underwood & Griggs 847 (F. MICH. NY. US). MAYAGUEZ Britton & Shafer 1832 (F. MO. NY. US), Chamberlain s.n. (F), Sintenis 763 (GH. US), Stimson 3272 (DUKE). PONCE Britton et al. 1768 (NY, US), Britton 8557 (F. GIL MO, NY, US), Heller s.n. (US), SAN JUAN Britton et al. 2855 (F. NY. US), Goll 857 (NY. US), A. & G. Heller 397 (F. NY. US).

Zamia pumila is distinguished from other species of the genus by its low stature, underground stems, unarmed petioles, sparsely toothed, often rounded leaflets, small, long-peduncled cones with rusty or purple pubescence, and low-faceted cone scales. Although all of these features are found individually in other species of the genus, the combination is unique to the West Indian plants. This species is most closely related to the Mexican and Central American Z. *Jurfieracea*, which differs in being more robust and in having larger, spiny-petioled leaves, tougher, more serrate leaflets, longer-peduncled cones with tawny pubescence, and smaller red seeds.

As noted above, Zania pumila subsp. pumila is very variable in leaflet form both within and between West Indian subregions. It was initially expected that varieties

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would be recognized within the subspecies. This would give some taxonomic recognition to the diversity, which is particularly troublesome in an area such as the Bahamas, where individual islands have distinctive, relatively homogeneous populations (Ficurus 7, 8; Eckenwalder, in press). This expectation was abandoned because of lack of morphological discontinuities in specimens of the subspecies from throughout its range. No coherent system of varieties could be devised that was not as arbitrary and as typological (in the perjorative sense) as the earlier systems of species here replaced with the present broadened concept. Local botanists are thus left with the somewhat unsatisfactory circumstance of not being able to give taxonomic recognition to distinctive variants that occur in their region and that integrade only in some less familiar ground. The capacity for long-distance dispersal by seawater has evidently aggravated this situation (Eckenwalder, 1980).

- Zamia pumila L. subsp. pygmaea (Sins) Eckenwalder, stat. et comb. nov. BASIONYM. Zamia pygmaea Sims. Bot. Mag. 43: 1.7741. 1815. Type: W. Indies [Cuba], cult. Hort. Loddiges, Salisbury s.n. (holotype, BM). Palmifolium pygmaeum (Sims) Kuntze, Rev. Gen. Pl. 2: 803. 1891.
  - Zamia kickvii Miq. Monogr. Cycad. 71. t. 8, fig. A. 1842. TYPE Cuba, cult. Hort. Ghent, Kickv s.n. (holotype, 1.). Palmifolium kickvii (Miq.) Kuntze, Rev. Gen. Pl. 2: 803. 1891. Zamia pygmaea var. kickvii (Miq.) Schuster, Pflanzenr. 99: 152. 1932.
  - Zania ottonis Miq. Linnaea 17: 740. 1843. Type Cuba, Matanzas, San Antonio Fundador de Caminar, Otto 36 (holotype, L. isotypes, B.NY (frag.)!). Palnifolium ottonis (Miq.) Kuntze, Rev. Gen. Pl. 2: 803. 1891. Zamia pygmaea var. ottonis (Miq.) Schuster, Pflanzenr. 99: 153. 1932.
  - Zamia pygmaea var. wrighti A. DC. Prodr. 16(2): 543. 1868. Type. Cuba, Sabanas Chirigati, Wright 3192 (holotype, GDC, isotypes, BM!, GH!, Mo!). Zamia chamberlainii Schuster, Planzen, 99: 153. 1932.
  - Zamia silicea Britton, Bull. Torrey Bot. Club 43: 462. 1916. Type Cuba, Isla de Pinos, vicinity of Los Indios, Britton, Britton, & Wilson 14166 (holotype, sv!; isotypes, Fl, Gul, us!). Zamia media var. commeliniana f. silicea (Britton) Schuster, Pflanzen: 99: 157. 1932.
  - Zamia rotundifolia Hort. ex Schuster, Pflanzenr. 99: 152. 1932, nomen inval. (pro syn. Z. pygmaea var. kickxii (Miq.) Schuster).

ILLUSTRATIONS Victorin & León, Itin. Bot. Cuba. figs. 113, 114, 173, 181, 189. 1942.

Cycads differing from subsp. *punila* primarily in smaller stature, with few differences of proportion; stems 0.5–2 cm. in diameter; leaves (0.5-)–1–4(–7) dm. long; leaflets 1–7(–10) cm. long, narrowly oblong to obovate, typically shorter and more numerous with respect to total leaf length than in subsp. *punila*, much thinner in texture and more fragile; male cones 1.5–5 cm. long; female cones 2.5–7 cm. long; seeds 1–1.5 cm. long. n = 8 (Norstog, in press).

DISTRIBUTION Dwarf cycads are endemic to western Cuba and Isla de Pinos (MAP 1) and intergrade with subsp. *pumila* castward across the main island (FiGURE 6). These cycads typically occur in open limestone and serpentine communities, but the most robust individuals grow in moist forests of ravines on isolated mogotes (limestone hills) from Pinar del Río Province to Las Villas Province. Here they may be replaced by subsp. *pumila*. They are uncommon in outlivation and are apparently relatively little affected by human activities.

REPRESENTATIVE SPECIMENS. Cuba. C-MAGUEY Britton 2386 (NY), Britton et al. 13166 (NY), Carabia 3405 (1), HABANA Britton et al. 638 (E-NY), 6267 (NY), Carabia 1869 (1), ISLADE PHONS Britton & Wilkon 14877 (NY, IS), Carabia 983 (1), Killip 42674 (GH, US), LAS VILLAS, Britton et al. 10233 (NY, US), Combs 647 (GH), Howard et al. 290 (A, LL, MICH, NY, UC), Luna 585 (E, NY), MATANZAS Britton & Wilkon 420 (NY), Carabia 1591 (F), Van Hermann 913 (E, NY), PINAR DEL RIO Britton et al. 9664 (NY, US), Shafer & León 13713 (E, GH, NY), Van Hermann 2652 (E, NY, UC).

Zamia pumila subsp. pygmaca is the smallest fiving cycad. Although the largest individuals overlap subsp. pumila in total leaf length, the leaflets are proportionately shorter and broader than on corresponding plants of the more widespread subspecies, the stems are more slender, and the male and female cones and seeds are somewhat smaller. Chambertain apparently crossed the two subspecies and obtained hybrids, some of which reached Fairchild Tropical Garden during the dispersion of his living collection after his death. These uncertainly documented plants appear intermediate, normal, and fertile. In all respects, plants of subsp. pygmaca resemble miniature versions of subsp. pumila. The differences are preserved after twenty years of cultivation at Fairchild Tropical Garden, so they are presumably genetically based. The evident similarity of the dwarf plants to subsp. pumila and their intergradation with the more robust plants argue against their recognition at a higher taxonomic rank.

#### INTRODUCED CYCADS

#### Zamia furfuracea Aiton, Hortus Kew. 3: 477. 1789.

Zamia gutierrezii Sauvalle, Anales Acad. Ci. Méd. Habana 5: 54, 1868. Twe-Cuba, Pinar del Río, cult. Hort. Blain, Rangel (holotype, nac.isotypes, r!, sv!). Zamia media var. gutierrezii (Sauvalle) Schuster, Pilanzen: 99, 154, 1932.

Palma pumila Miller, Gard. Dict. ed. 8. no. 9. 1768. LECTOTYPE Palma fructu clavato polypreno, C. J. Trew, PI. Selec. t. 26. 1752?

As noted both by Carabia (1941) and in correspondence associated with herbarium specimens at oit, this Mexican and Central American species has been cultivated for more than a century in the West Indian region. Plants growing in what was once a botanic garden in Cuba were renamed by Sauvalle and were considered as a West Indian endemic. Schuster (1932) incorrectly believed that these represented the widespread, particularly robust phase of Zamia pamila subsp. pamila (called Z. *Latifoliolata* Prenl. by many authors) and made a combination appropriate to that view. Zamia furfuracea is contrasted with Z. pumila in the discussion of subsp. pumila. The two species may hybridize when brought together, and putative hybrids of this parentage can be found at Fairchild Tropical Garden.

Cycas circinalis L. Sp. Pl. 2: 1188. 1753.

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Cycas revoluta Thunb. Fl. Japon. 229, 1784. Cycas rumphii Miq. Bull. Sci. Phys. Nat. Néerl. 2: 45, 1839.

The familiar Asiatic sago palms are widely cultivated in the West Indies, as in all tropical and subtropical regions. They are arborescent cycads readly distinguished from the native plants by their leaflets with a midrib, and by their large seeds borne on elongate sporophylls not aggregated into compact cones but appearing in flushes alternating with flushes of foliage leaves. These most-isolated cycads are often retained as the sole extant genus of Cycadaccae, while other genera with distinct, pedunculate, megasporangiate strobili (Johnson, 1959) are segregated to the Zamiaccae (and Stanceriaccae).

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